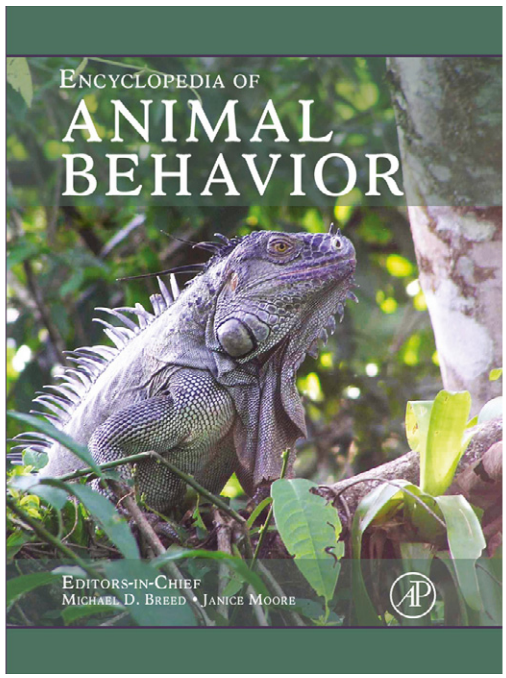

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Magnetic Compasses in Insects

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Introduction

The use of magnetic information as a compass is among the most intriguing mechanisms used by animals to orient and navigate. Part of our fascination with the use of magnetism comes from our inability to perceive it relying only on our sensory machinery. In recent decades, we have seen a burst of interest and research on how animals detect and use the Earth's magnetic field. This article focuses on our current knowledge on the use of magnetic information as a compass for orientation and navigation in insects.

The use of magnetic information in insects was first recognized in the late 1950s, with alignment of the body axis in termites relative to the Earth's magnetic field. During the 1960s, interest in the alignment behavior increased, and several other species belonging to taxonomic insect Orders as diverse as Diptera, Coleoptera, Orthoptera, and Hymenoptera were added to the list of insects with magnetic sensitivity. Although it has been difficult to interpret the biological meaning of such alignments, their discovery initiated further studies on the use of magnetic compasses. The discovery of bacteria, with magnetite crystals causing them to move in alignment with the Earth's magnetic field, stimulated the search for magnetic compasses in a diversity of vertebrates and invertebrates, based on similar principles. Also, the continued analysis since the 1970s of the use of magnetic information by model insect species, such as the honeybee *Apis mellifera* and the fruit fly *Drosophila melanogaster*, not only showed that magnetic fields could be used under diverse contexts but also motivated the exploration of such capacities in other insect species. Thus, during the 1980s and 1990s, research turned toward the search of a magnetic compass for navigation. Of particular interest were the species exhibiting long-distance migrations, which were predicted to rely on prominent compasses available across the unknown terrains of their migratory routes. This interest was further supported by additional findings of magnetic particles in insect tissues, which could become the substrate for the compass.

However, determining the use of a magnetic compass has not been an easy task. Part of the problem is that magnetic compasses do not seem to be the primary tools within the multimodal systems of navigation. Thus, the role of the magnetic compass is often uncovered only after other sources of information, such as the sun or other significant landmarks, are unavailable or unreliable. On the other hand, experimental manipulations are constrained by our lack of understanding of the mechanisms underlying the magnetic compass. These two main problems have become the focus of research in the new millennium. First, the analysis of central place foragers, such as honeybees and ants, has allowed for controlled manipulations uncovering interactions of the magnetic compass with other navigational mechanisms. Second, model species, such as cockroaches, honeybees, and fruit flies are becoming essential for the understanding of proximate causes. Particularly remarkable in this respect is the use of genetic manipulations in the fruit fly *D. melanogaster*.

In general, understanding the use and role of magnetic compasses requires comprehension at different levels, from the nature and source of the magnetic cues to the mechanisms of perception, including the nature of the compass and interactions with other cues during the process of decision-making. Our current knowledge of these levels appears as a puzzle, where behavioral studies have contributed with most of the pieces.

What Is Special About Magnetic Information?

The primary source of magnetic information is the iron-rich molten core of the Earth, which makes it hold an enormous magnetic field with lines of force running from magnetic South toward the North Pole (conventionally named north and south relative to the geographic north and south, respectively). The magnetic lines of force vary in inclination, pointing upward in the southern hemisphere, parallel to the Earth's surface at the magnetic equator,

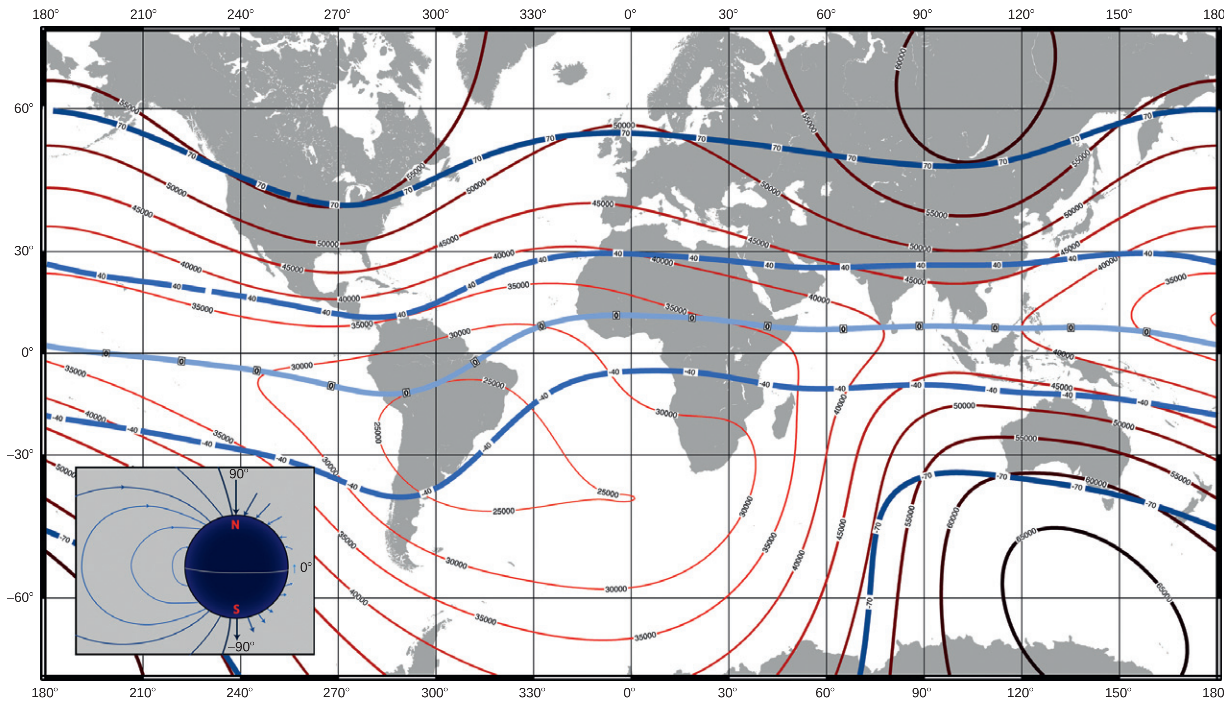

Figure 1 A projection of the Earth derived from the World Magnetic Model (http://www.ngdc.noaa.gov/geomag) showing the intensity of magnetic flux in shades of red and the magnetic inclination from the magnetic equator to the poles in shades of blue. The North and South magnetic poles are not shown because the map ends at the eightieth parallels. Inset: A diagram showing the trajectory of the magnetic field from the southern geomagnetic pole to the northern geomagnetic pole. The equatorial line is the geographic equatorial line and so the inclination is zero on the line in only two locations (i.e., where the light blue line crosses the equatorial line at ca. 315 degrees and at ca. 200 degrees).

and downward in the northern hemisphere (Figure 1). Thus, these lines of force have both horizontal and vertical components, which can potentially be used by compasses. The horizontal parameter is easily described by the North–South polarity, whereas the vertical component is called inclination and depends on the angle at which the line of field at a particular location meets with the horizontal plane of the Earth's surface. Inclination roughly correlates with latitude, decreasing from the poles where it is 90° (+90° at the magnetic north pole and −90° at the south pole) to 0° at the magnetic equator which roughly corresponds with the geographic equator. A third component of the Earth's magnetic field is its intensity, with its maxima at the magnetic poles and minimum at the equator. Although two positions are at the same latitude, it is likely that they will have unique inclinations and intensities, such that an animal with the ability to sense both of these features may be able to use them as beacons identifying its position. Importantly, in addition to the global pattern of the Earth's magnetic field, local deposits of iron may interfere with the Earth's magnetic field, creating magnetic anomalies, which serve as beacons for orientation, navigation, and the construction of maps of local magnetic information.

From the previous description, several particularities of the magnetic information can be drawn. First, it is continuously available everywhere on Earth. This marks a difference with, for instance, solar information, which is intermittently available above the ground and never available below the ground. Second, it is intrinsically directional in one of its components, with such directionality being relatively stable overtime (even after considering the changes in declination from 1 year to the next and the flipping of the magnetic poles in geological time). And third, it is spatially variable in two of its parameters (vertical component and intensity).

For What Purposes Do Insects Use a Magnetic Compass?

Body Alignment and Nest Construction

Body alignment refers to the preference of individuals to orient their body axes relative to the lines of force of the magnetic field. In most cases, insects align themselves parallel or perpendicular to the field, but some intermediate orientations have been reported. Early studies found body alignment in flies (Diptera) and termites (Isoptera) at rest. Body alignment has also been observed in bees and wasps (Hymenoptera), beetles (Coleoptera), crickets, and cockroaches (Orthoptera). Body alignments are evaluated by rotating or canceling the local magnetic field (a magnetic coil design that might be used to reverse the

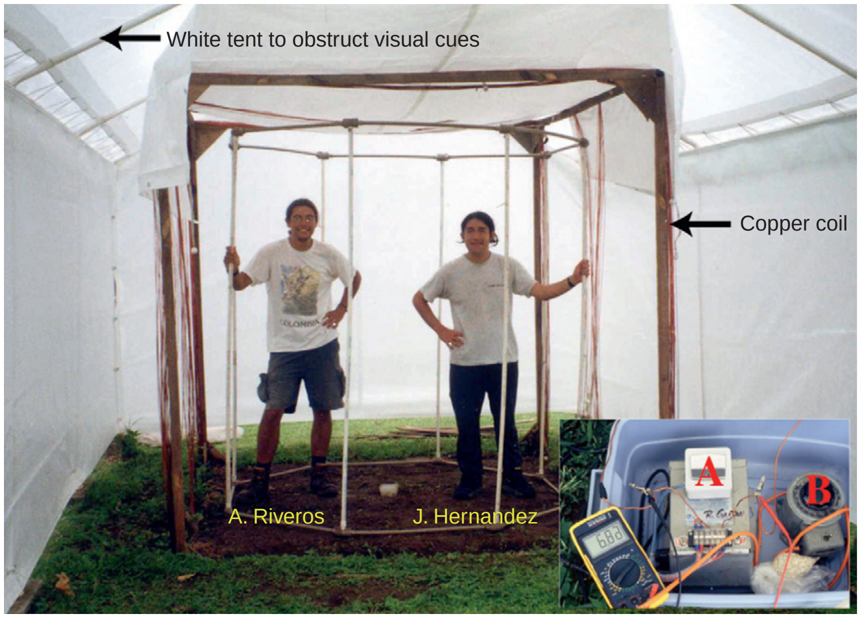

Figure 2 A wood frame constructed with brass screws holds the copper wires wound in a Merritt 4-coil construction. The coil is positioned around the geomagnetic North–South axis. We transformed AC to DC electricity to power the coil with sufficient current to reverse the horizontal component of the Earth's magnetic field. A white tent surrounds the coils to obstruct celestial cues and landmarks on the horizon. The PVC frame can hold a nylon net to prevent insects from escaping, and in the floor of the arena is a camera to observe the insects from a remote location. *Inset:* (a) AC–DC transformer; (b) Variac.

horizontal component of the Earth's magnetic field is shown in Figure 2). Under the experimental condition, an animal preferring a particular orientation aligns according to the artificial field; if the field is compensated, the preferences disappear. Following the manipulation, the animal realigns to the natural field.

Although typically associated with resting behavior, body alignments may also be involved in more complex contexts. In some cases, body alignments may be overridden by other cues and may represent an adaptive, rather than a passive, response. Three remarkable examples are nest construction in honeybees and termites, alignment of waggle dances by honeybee foragers, and nomadic movements of the nomadic ant *Pachycondyla marginata.*

During nest construction, compass termites (*Amitermes meridionalis*) orient their gigantic mounds of northern Australia on the North–South axis (with some regional variation reported). Similarly, honeybees seem to rely on magnetic information during comb construction as suggested by the irregular combs built when magnetic alterations are experimentally introduced. In both species, the use of magnetic information during nest construction has been associated with the absence of directional cues in the dark and the need to coordinate many individuals involved in the task. Furthermore, in compass termites, the preference for the North–South axis may benefit nest thermoregulation, maximizing exposure to the sun during mornings and afternoons and minimizing it at noon. Indeed, regional variation in orientation is related to the environment in such a way as to suggest that nest alignments with the magnetic field are adaptive.

A preference for a magnetic axis is also evident during the waggle dance of the honeybee. Foragers dance to communicate to their hive mates the direction of a resource by transposing the angle between the sun and the resource to the angle between the gravity and the axis of their dance. The directions communicated exhibit systematic errors that vary across the day (with the position of the sun). Such 'misdirections' disappear if the magnetic field is compensated, or if the direction toward the resource coincides with the cardinal directions. Thus, the waggle dance seems to reflect the preference of the honeybees to align with the magnetic field, as also observed during comb construction or when they are at rest.

A colony of nomadic ants *P. marginata* relocates its nest with a preference to move on a North–South axis. Relocation of nests is associated with the capture of their only prey, the termite *Neocapritermes opacus.* Following relocation, they forage on either side across their migratory axis, enabling colonies to minimize overlap with areas that were previously searched.

Tropotactic-Based Navigation

In tropotactic behavior, insects move toward or away from a stimulus, such as light, humidity, or temperature. Such movements typically lead the animals to more favorable conditions within relatively short distances. In cases where the directional stimulus and the magnetic field are spatially associated, an animal may substitute use of the latter as a directional cue if the primary stimulus is absent or lacks directional information.

For example, fruit fly (*D. melanogaster*: Diptera) larvae exhibit negative phototaxis during their first three developmental instars, but when they begin to search for a pupation site, they switch to positive phototaxis. In the right experimental setup, the light's direction can be associated with the direction of the magnetic field. After experimental shifts of the field, fruit fly larvae reorient as predicted.

As another example, mealworms (*Tenebrio molitor*: Coleoptera) show positive phototaxis in low or high relative humidity, and negative phototaxis in intermediate conditions. Similar to fruitflies, the light's direction can be associated with the direction of the magnetic field. This has been verified by shifting the magnetic field under homogeneous lighting or in the absence of light. Under homogeneous light conditions, adult mealworms moved toward the predicted direction of greater or lesser light that was indicated by the rotated magnetic field, whereas they oriented randomly in darkness.

Central Place Foraging

Central place foraging is a challenging task that involves displacements between home and particular resources, typically food and mating areas. This implies that movements occur within a more restricted area than migrations, which allow animals to rely on their memory to recognize particularities of the terrain (e.g., visual landmarks). Within insects, research on the use of a magnetic compass during central place foraging has focused on the species of Hymenoptera, particularly ants and bees, and Isoptera (termites).

The use of a magnetic compass during foraging is suggested by the ability of certain species to navigate home even when cues, such as sunlight and landmarks, are absent. Often, central place foragers may be evaluated in a natural context in which the location and nature of the goal is specified by the experimenter. Under these conditions, foragers are typically trained to visit a feeder where either the external state is manipulated (e.g., exposure to reversed fields or training to experimentally produced magnetic anomalies) or their internal state is altered with strong disruptive fields (e.g., a brief magnetic pulse, Figure 3 or a strong bar magnet, Figure 4).

Training in a discriminative paradigm has been used in the honeybee *A. mellifera*. Honeybee foragers can be trained to recognize the location of a food source based on differences between two locally produced magnetic fields. The repeatedly successful replication of this paradigm has proved that honeybees can rely on magnetic cues during foraging; yet this is not the only proof of such capacity or the only context in which honeybees use magnetic information.

Figure 3 Pulse magnet treatment of a migrating *Urania* moth captured flying across the Panama Canal. Should the compass be composed of single domain magnetite and arranged in a similar way to that in the magnetotactic bacteria, this treatment will reverse the geographic orientation of the moths upon release.

On the other hand, manipulations of the horizontal component may include a total reversal (180°) or a partial shift (typically 90°) of the magnetic polarity. Between these two variants, the partial switch is preferred because the total reversal may lead to axial distributions that are more difficult to interpret. Nevertheless, both manipulations have successfully provided evidence for the use of a magnetic compass in insects. Carpenter ants and honeybees turn their orientations in experimental arenas according to the artificial magnetic shifts (magnetic field turned 90°). Similar changes are observed in termites when fields are shifted even less than 45°. On the other hand, under complete reversal of the magnetic polarity, foragers of weaver ants and leaf-cutter ants shift their homing orientation ~180° relative to bearings of control individuals, demonstrating that they can rely on a magnetic compass for homing when other cues are absent.

However, insects do not rely on magnetic compasses only when information from other compasses is not available or reliable. This seems to be true particularly for central place foragers, which, as mentioned before, navigate within a familiar area. In this case, alternative mechanisms, such as landmark navigation, pheromone

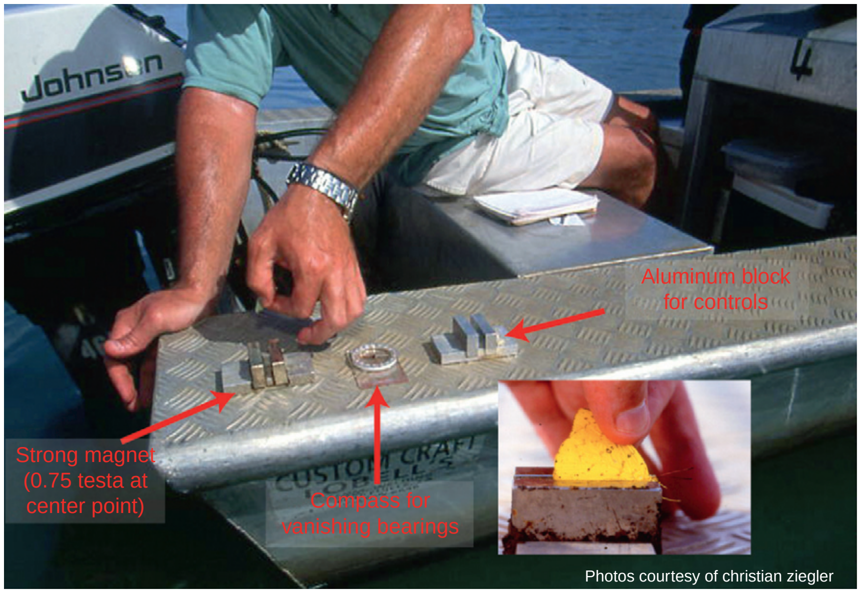

Figure 4 Strong magnet treatment of migrating butterflies captured flying across the Panama Canal. *Inset:* Detail of a butterfly during exposure to a strong magnet bar.

trails, or path integration, may be suitable enough for foraging and homing; yet, those mechanisms may interact with, or be supported by, a magnetic compass. Indeed, a path-integrated vector can be updated by the use of a magnetic compass in leaf-cutter ants, as demonstrated by the shift in the vector home after a reversal in the magnetic polarity or by the inability to orient homeward after exposure to a strong magnet.

The use of landmarks may also be supported by a magnetic compass. During route learning, honeybee foragers should recognize the location of the landmarks on the terrain based on a directional framework. Although a sun/sky compass may efficiently provide such a framework, a magnetic compass may act as an alternative if other cues are not available. The magnetic compass also has the advantage of providing an unambiguous system when compared, for instance, with a polarized sky. Magnetic compasses may be of major importance for species living in the forest or in the dark, where landmarks are certainly available but neither the sun nor the sky can be reliably used. Indeed, termite foragers use a magnetic compass in conjunction with pheromones, in order to determine the trail's polarity and indicate the goal's direction.

Long-Distance Migrations

All the features described before have made the magnetic field a recurrent candidate to be a directional cue for long-distant migrants. Within insects, long-distant migrants include species of dragonflies, beetles, butterflies, moths, and locusts. In some of these insects, observations of directed migrations in the absence of celestial cues, such as sunlight, have been used to suggest the use of a magnetic compass. This is the case for migratory butterflies, such as the monarch butterfly *Danaus plexippus* or the sulphur butterflies *Aphrissa statira* and *Phoebis argante*, all of which can orient with a sun compass, but are also observed migrating directionally under overcast skies. It is also the case for some migratory moths, such as the silver Y *Autographa gamma*, which maintain migratory directions on moonless nights.

Results from experiments manipulating the magnetic environment and from experiments disrupting the compass support the hypothesis that insects may use a magnetic compass for long-distant migrations. In Neotropical butterflies, natural migratory orientation is altered after exposure to a strong magnet (Figures 4 and 6). Also, orientation relative to migration can be reversed when the magnetic polarity is experimentally reversed (by a coil such as in Figure 2). Although in these manipulations, control groups do not always follow their natural directions of migration, the significant differences with treated groups suggest sensitivity of the compass to the experimentally manipulated magnetic field. In addition, magnetite crystals have been detected in the body of monarch butterflies and at least one of the Neotropical migrating butterflies (*A. statira*, see 'Properties of the Insect Magnetic Compass').

Of course, magnetic information is not necessarily the only or the primary mechanism that migrants may rely on. This fact makes the study of interactions between compasses an exciting field of research but complicates the experimental evaluation of a magnetic compass, especially in the field, where factors, such as weather and alternative navigational cues (e.g., landmarks, sun), are difficult to control. Therefore, field studies are often combined with laboratory manipulations; yet more controlled environments are not completely safe from confounded effects or lack of motivation of the animals.

Properties of the Insect Magnetic Compass

The use of a magnetic compass requires several steps, from the acquisition (perception) of the information to its transduction and subsequent use during the process of decision-making. Our current understanding of these levels includes mainly behavioral evidence for the perception of the magnetic information and, in some cases, how such information interacts with other cues. To date, we lack a complete understanding of the mechanistic processes underlying the perception of magnetism and its integration into multimodal strategies of navigation. For example, it has only rarely been tested whether insects detect polarity from the horizontal component of the Earth's magnetic field or from its inclination. Honeybees and ants obtain polarity information from the horizontal component of the Earth's magnetic field, but recently, flour beetles *Tenebrio* sp. were shown to use the inclination of the magnetic field relative to gravity for short distance movements.

The discovery that magnetotactic bacteria use chains of single-domain magnetite to cause them to move along the lines of magnetic flux stimulated the search for magnetite in animals. The mechanism for a compass based on single-domain magnetite is similar to our anthropogenic compass. The magnetite crystals are rotated to align with the magnetic field, providing the animal with information on the field's polarity. Although the mechanisms for neural transduction have never been verified, it is hypothesized that magnetite chains are attached to ion channels so that magnetically induced realignments would lead to opening of the channels and cell depolarization.

Support for the use of a magnetite-based compass comes from both behavioral assays and the presence of particles of magnetite in different species. Interestingly, the presence of magnetite is not exclusively associated with any organ in particular, and within an individual, it is not limited to a particular area. Its presence has been shown in diverse body areas such as the abdomen (e.g., honeybee *A. mellifera*), the thorax (e.g., monarch butterfly *D. plexippus*), the antenna (e.g., nomadic ant *P. marginata*, stingless bee *Schwarziana quadripunctata*), and the head (e.g., fire ant *Solenopsis invicta*).

Recently, a second magnetite-based configuration for sensing magnetic fields has been proposed for honeybees. In this system, variations in the field intensity are associated with changes in the size of magnetic granules (located inside iron deposition vesicles of trophocytes). Increases in field intensity lead to shrinking of magnetic granules in a direction parallel to the applied field and to their expansion perpendicular to the applied field. Furthermore, such changes in the magnetic granule's size are associated with intracellular release of calcium from the trophocytes. As iron deposition vesicles are attached to the internal cytoskeleton, it is proposed that changes in the magnetic granules' sizes induce relaxation or contraction of the cytoskeleton, which in turn, lead to the release of calcium ions for signal transduction.

The radical pair compass is a mechanism proposed for sensing magnetic fields without magnetite. Photosensitive molecules are excited by the incidence of light, and an electron is elevated to the singlet excited state. Singlet radical pairs form with antiparallel spin, and there is a reversible conversion of singlet radical pairs with antiparallel spin to triplet radical pairs with parallel spin. The equilibrium state of the reversible reaction forming the two radical pairs depends on the alignment of the sensory system to the earth's magnetic field. Presumably, the animal could sense the orientation of the magnetic field by comparing the amount of conversion from singlet to triplet radical pairs in different orientations. The conversion of singlet to triplet radical pairs would be symmetrical around the axial vector of the magnetic field, and thus serve as an inclination compass. Since photopigments, such as opsins, do not form radical-pairs in reaction to light, it has been proposed that other molecules, specifically cryptochromes, may be involved in the magnetoreception. Within insects, cryptochromes are found in the fruit fly *D. melanogaster*, which, accordingly, has a light-dependent magnetic compass.

Indeed, a direct connection between cryptochromes and magnetic sensitivity was recently determined in fruitflies. In a T-maze paradigm, fruit fly adults can be trained to associate the presence of a magnetic alteration with a food reward. Wild strains thoroughly learned the association, whereas Cry mutants (i.e., cryptochrome-lacking mutants) failed in the task. Wild strains that were trained in light spectra that do not activate the cryptochromes also failed in the learning task.

Future Challenges and Prospects

We have emphasized throughout this article that in order to understand orientation by insects with magnetic compasses, we need to integrate how the information is sensed, how it is perceived and processed, and how the animal uses and responds to the magnetic information. The integration of those levels is probably one of the most interesting challenges for the near future.

First, we are in need of developing and refining the methodologies for the evaluation of the magnetic sensory system. We currently lack replicable behavioral paradigms enabling the simultaneous evaluation of neural activity while magnetic information is experimentally manipulated. Recent attempts aiming to standardize behavioral assays have relied on alignment behavior in cockroaches, which might be used under more restrained conditions (e.g., for electrophysiology recordings). However, a magnetic compass involved in body alignment may involve completely different sensory organs and neural wiring relative to that involved in goal orientation. We have not yet found a specialized organ for sensing magnetic information in insects. Concentration of magnetite in the head and antennae indicate that these sections might play a role in the magnetic perception of certain species. Research that focuses on the antennae and other body parts accessible for electrophysiological recordings will hopefully improve the chance of isolating the relevant sensory tissues.

For example, the protein-stringing magnetite vesicles onto the bacterial cell filament is known to be mamJ. Researchers have suggested that a general survey of the Animal Kingdom be conducted for other species that express mamJ. Similarly, an antibody to mamJ could be used as a marker to structurally link magnetite crystals to neural cells. For example, magnetite has been observed with electron microscopy in the antennae of the nomadic ant *P. marginata*. Is mamJ also expressed in the same general region and can it be associated with neural synapses?

In the previous section, we discussed the lack of research on a compass based on the polarity of the magnetic field versus a compass based on inclination. If only the horizontal component of the magnetic field is experimentally changed, one cannot distinguish the two types of compasses. A complete experimental protocol would include a natural control, changing the horizontal component without changing the inclination, and reversing the inclination without changing the horizontal component (**Figure 5**). The experimental setup can be accomplished with two overlapping coils – one oriented about the polarity vector and another oriented about the vertical flux.

Second, as the magnetic compass is part of a multimodal system of navigation, research on the hierarchical and supportive interactions with other mechanisms warrants further experimental efforts. Many animals rely on more than one compass, with the sun being a typical reference for diurnal insects. African dung beetles orient with polarized moonlight. When more than one compass is invoked, they may conflict with one another. For example, both the sun and moon compasses are based on the rotation of the Earth about its geological poles, whereas

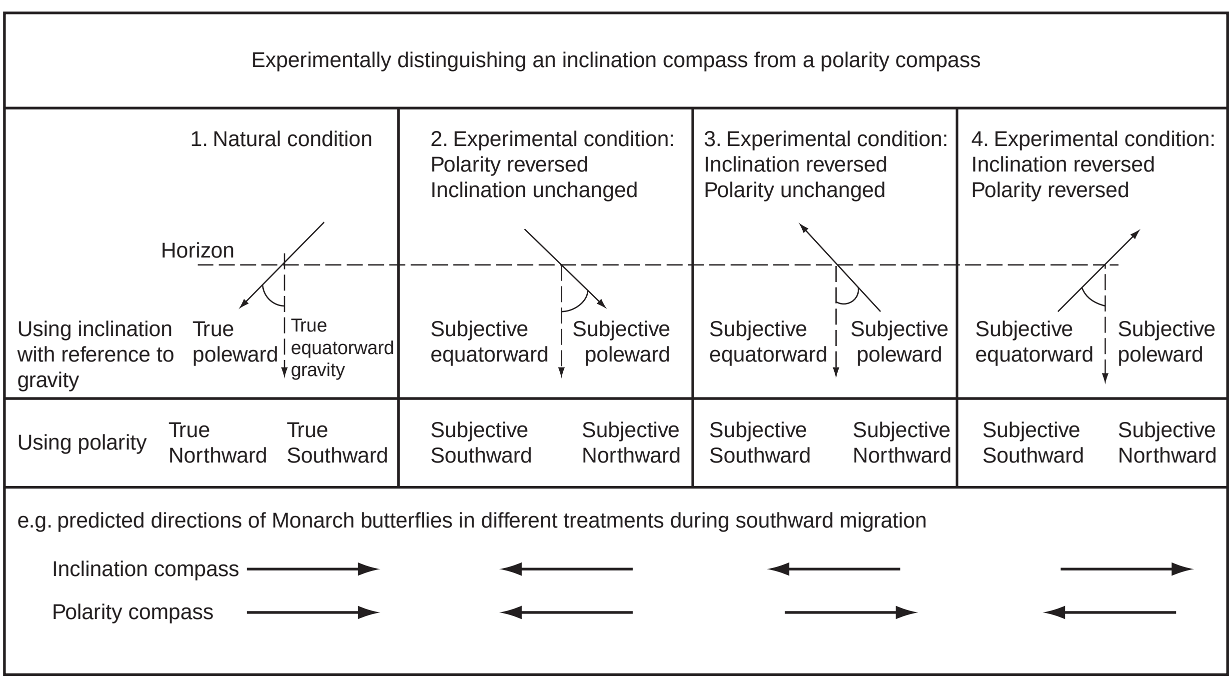

Figure 5 Manipulations of the local magnetic field to distinguish a polarity compass from an inclination compass. Experiments would include a natural control, changing the horizontal component without changing the inclination (which will alter insect orientations whether a polarity compass or an inclination compass is operating), reversing the inclination without changing the horizontal component (which will alter insect orientations if they use an inclination compass but not if they use a polarity compass), and reversing both the inclination and the horizontal component (which will alter insect orientations if they use a polarity compass but not if they use an inclination compass).

the magnetic compass is based on the geomagnetic poles (true North lies in the Arctic Ocean, whereas magnetic North is offset 11° latitude onto the Canadian island of Ellsmere). The difference in orientation between the geological and geomagnetic axes is called declination and varies with location on the Earth. In short range movements, declination will not be an issue, but over long distances, animals that use both a sun and a magnetic compass must calibrate one with the other.

Over the longer term, the geomagnetic poles are not stable points. Declination changes on an ecological timescale and the poles may reverse on a geological timescale (on the order of one-half million years). The most recent reversal was 750 000 years ago. For long-distance migrants, the Earth's magnetic poles are stable within a generation, but an insect, such as a monarch butterfly, must have a means to reach its winter destination site in central Mexico encoded genetically. Thus, whether the insect's preferred magnetic compass headings are plastic or hard-wired will be important to its success at reaching its destination. Finally, sunspot activity can disrupt the Earth's magnetic field creating magnetic anomalies that ebb and wane on a 11-year cycle. For example, orientation of stingless bees *S. quadripunctata* at their nest entrance was altered by a magnetic storm in 2001. How do animals cope with changes in declination and magnetic anomalies?

Third, how might insects use the magnetic field? Monarch butterflies east of the Rocky Mountains must carry the genetic blueprint necessary to fly from natal grounds to an overwintering site in the mountains of Michoacan, Mexico, as far as 5000 km away. Elaborate hypotheses for how they navigate en route involve the use of geomagnetic information. One particularly interesting feature is a magnetic anomaly at their destination that may guide their final approach like a beacon. On a more local scale, honeybees have been trained to detect spatial anomalies associated with nectar rewards, which can be used to measure their sensitivity to differences in magnetic fields or to set up experiments where orientation cues conflict with one another.

We need to make experiments as natural as possible to investigate how insects use the magnetic field. Tethering of insects confounds body alignment with goal orientation, orientations that may involve different sensory tissues and neural processing. Arenas that obscure celestial cues and landmarks cause insects to lose motivation to move toward a goal and attempt to escape instead. Insects that migrate for long distances or at high altitudes are notoriously difficult to study in these artificial settings. We have successfully tracked naturally migrating butterflies, *Urania* moths, and dragonflies, as they flew over bodies of water, by following them in a boat. We have also conducted releases of butterflies and day-flying moths over water in order to conduct experiments in an open environment that is as homogeneous as possible (**Figure 6**). However, the boat has its limitations of distance, and for nonmigratory species, a body of water could be an unnatural setting. Radio transmitters are becoming lighter in weight to the point that dragonflies and other migratory insects can be followed remotely (**Figure 7**), and the launch of low-orbiting satellites to track insects with satellite transmitters is on the horizon in project ICARUS (International Cooperation for Animal Research Using Space).

The use of animal models, such as the fruitfly *D. melanogaster* or the honeybee *A. mellifera*, will certainly be of major relevance. This is exemplified by the recent genetic manipulations affecting the magnetic compass in *Drosophila* adults and providing us with a more detailed understanding of the mechanistic perception of magnetic information. Having genetic tools to integrate levels from sensory input to information processing and behavior output seem very promising. Nevertheless, it is also very important to consider the limitations of traditional models

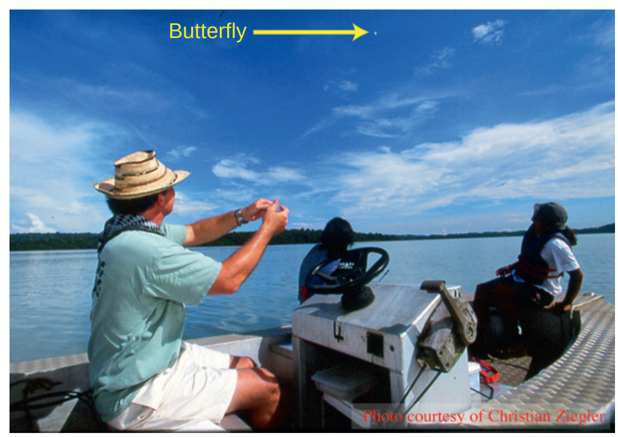

Figure 6 A butterfly released over the Panama Canal. Following manipulation of its internal state with a strong magnet, we measure the compass orientation on the horizon at which the insect vanishes (a vanishing bearing).

Figure 7 A migrating Mormon cricket *Anabrus simplex* (Orthoptera) with a radiotransmitter glued to its thorax.

in aspects such as experimental manipulations and the extent to which they enable generalizations (i.e., at what degree they are really models). This is particularly true as our knowledge of the diversity of magnetism-associated behaviors increases. An example is the difference between magnetite and light-based magnetic compasses. Thus research on species, such as *Drosophila*, may shed light on the processing of magnetic information, but it may remain limited to those insects with a light-based magnetic compass.

Therefore, the exploration of magnetic compasses in other species is warranted. Increasing the range of species not only enables the evaluation of the taxonomic distribution of magnetic compasses but, importantly, it might provide us with more suitable models for specific questions. In this respect, the use of nocturnal species appears promising, since other relevant mechanisms of navigation, such as a sun compass or landmark navigation, are naturally controlled and, of course, those species might adopt the magnetic compass as the primary mechanism. A complete understanding of orientation by the magnetic compass will also provide a better comprehension of insect cognition such as decision-making, learning, and memory.

See also: Insect Migration; Insect Navigation; Magnetic Orientation in Migratory Songbirds.

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